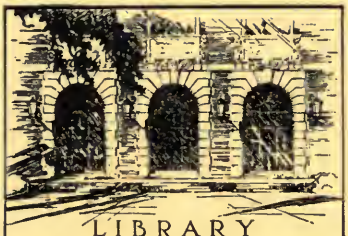
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The Morphology of the Swim Bladder and Auditory Bulla in the Holocentridae

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INTRODUCTION

The Holocentridae, squirrel-fishes, represent a family of marine fishes in the order Beryciformes. A few fairly well-defined genera make up this family. Although a number of genera have been erected upon larval forms, these have not been considered in this study. The two principal genera, *Holocentrus* and *Myripristis*, are circumtropical in distribution, while the secondary genera are more restricted geographically.

As early as 1829 Cuvier and Valenciennes described in general terms the relationship between the swim bladder and the posterior portion of the skull in the Atlantic form *Myripristis jacobus*. Interestingly enough they also suspected for this arrangement a possible auditory function such as E. H. Weber had described in 1820 for certain ostariophysine fishes. This condition was also noted for *Myripristis occidentalis* by Starks (1908). Starks (1904) and Regan (1911) described the auditory bulla in a few holocentrids. Subsequently Starks (1908) split the genus *Holocentrus* into two genera on the basis of the relationships of the swim bladder to the auditory bulla in the two forms on which he was working.

This paper represents a more detailed and complete study of the morphology of the swim bladder and auditory bulla in a more representative sample of the family (see list). It is part of a general study concerned with the relationships of the swim bladder to the inner ear of fishes.

I take great pleasure at this time in acknowledging the assistance given me in this problem by various institutions and persons. Both

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Chicago Natural History Museum and the United States National Museum generously gave me space in which to work and allowed me the use of their specimens. The Museum of Comparative Zoology of Harvard University lent me a specimen of the rare genus *Corniger*. Mr. Loren Woods of Chicago Natural History Museum pointed out the problem originally and handled the systematics. He was also very helpful in many conversations during the progress of the work. Miss Margaret Bradbury of Chicago Natural History Museum executed the figures. Mrs. Frieda Nelson assisted in the making of the serial sections.

GENERAL SYSTEMATIC RELATIONSHIPS

On the basis of the morphology of the swim bladder and the auditory bulla, their relationships, and the opisthotic bone in the forms studied, a natural dichotomy of the genera in the Holocentridae is indicated. The two major groups would be equivalent to subfamilial status (at least) and will be so treated here. One group, the Myripristinae, contains the genera *Myripristis*, *Holotrachys*, *Plectrypops*, *Ostichthys*, and *Corniger*. The second group, the Holocentrinae, contains the sole genus *Holocentrus*. This latter group is divisible in such a manner as to include the species *H. ascensionis* and its related form *H. rufus* as one subgroup and all of the other species of *Holocentrus* studied as a second general subgroup.

ANATOMICAL FINDINGS

A. *The Swim Bladder*

The swim bladder of the holocentrids has the usual two layers, the *tunica externa* and the *tunica interna*. The *tunica externa* consists of a heavy, white layer of circular fibers. It is generally attached firmly to the dorso-lateral aspects of the body cavity and anteriorly to the proximal portions of the pleural ribs and the bases of the vertebrae. It is somewhat thicker ventral to these attachments. The *tunica interna* is a thin, transparent inner lining of the swim bladder. In all of the forms studied the swim bladder is relatively large, occupying a considerable portion dorsally of the extra-peritoneal body cavity. In none of the specimens studied was there found a pneumatic duct connecting the swim bladder to the gut. A short, thick blood vessel and nerve were found in this region however, branching from the blood and nerve supply of the gut. Where

they entered the *tunica externa* on the ventral surface of the swim bladder, they made a well-defined aperture.

In the Holocentrinae, generally (pl. 1, fig. 2) the swim bladder is a simple tubular structure extending the entire length of the body cavity. Its anterior end is bluntly rounded.

In *H. ascensionis* and *H. rufus*, on the other hand (pl. 2, figs. 2 and 4), the anterior end is somewhat grooved between a pair of antero-lateral bulges. On the anterior face of each of these bulges the majority of the fibers of the *tunica externa* swing medially and laterally, thus thinning out this anterior surface and forming with the *tunica interna* a thin membranous area.

In the Myripristinae (pl. 3, figs. 2 and 3), the swim bladder is constricted between the anterior third and posterior two-thirds of its length so as to form two more or less individual "chambers" with a narrow, open connection between them. These "chambers" are not homologous with the chambers of many other forms (such as the Catostomidae and Characinidae) wherein one chamber develops as a process of another. In the Myripristinae it is a matter of constriction of a single-chambered swim bladder. The anterior "chamber" in addition has a pair of antero-lateral projections extending forward. These projections bulge laterally and have a flat surface facing medially. The *tunica externa* is thin on this flat surface and with the *tunica interna* forms a thin membranous area.

With the use of a limited series of *Myripristis* young, it was demonstrated that the antero-lateral projections develop during the early larval stages (10–30 mm. standard length). These projections grow forward from the antero-lateral corners of the swim bladder to either side of the posterior cranium. The specimen of *Ostichthys trachypoma* was a larval stage (24 mm. SL) and had not as yet effected the connection between the swim bladder and auditory bulla, but would nevertheless fit the Myripristinae pattern.

B. *The Auditory Bulla*

The auditory bulla is an enlarged portion of the otic region of the skull. In the Holocentridae, it contains a much enlarged sacculus with its otolith, the sacculolith (sagitta), oriented in an antero-posterior vertical plane. The lagena is a small outpocketing of the postero-dorsal region of the sacculus and is embedded in the bone of the cranium floor. In the larval forms, the lagena is relatively

large as compared to the sacculus; however, with growth the sacculus becomes the largest element, occupying all of the auditory bulla. The auditory bulla communicates widely with the cranial cavity and its opposite member in its middle portion.

In the Holocentrinae, generally the auditory bulla varies from a slightly elevated area on the lateral surface of the otic region to a considerable convexity of this region. In all cases, the auditory bulla has a membranous area facing laterally. This area is bounded by the prootic, exoccipital, and basioccipital bones (pl. 1, fig. 3).

In *H. ascensionis* and *H. rufus* (pl. 2, figs. 3 and 5), the auditory bulla is an elongated, tubular structure whose membranous area faces posteriorly. This tubular effect is primarily a function of an elongation of the prootic bone.

The auditory bulla of the Myripristinae (pl. 3, fig. 4) is much like that of the Holocentrinae. Its membranous area faces laterally. The main difference is in the fact that the margins of this membranous area are turned outward phlange- or lip-like.

C. *The Relationships of the Swim Bladder and the Auditory Bulla*

Within the family Holocentridae, three distinct types of relationships exist between the swim bladder and auditory bulla. In the Holocentrinae, generally (pl. 1) the anterior end of the swim bladder abuts against the thickened vertical septum, which is fixed transversely across the anterior end of the body cavity and separates the body cavity from the pharyngeal cavity. This, plus the fact that the membranous area of the auditory bulla faces laterally, constitutes a type in which no direct relationships are evident.

In *H. ascensionis* and *H. rufus* (pl. 2), the anterior bulges and the elongated auditory bulla are so disposed as to effect an intimate contact between the membranous areas of both.

The third type of relationships is that to be found in the Myripristinae (pl. 3). Here the membranous area of the medially directed, flat surface of the antero-lateral projection of the swim bladder forms an intimate contact with the laterally directed membranous area of the auditory bulla. In addition, the *tunic externa* makes a strong connection with the periosteum of the bony lip-like margins of the membranous area of the auditory bulla.

D. *Associated Structures*

In all of the holocentrid fishes, a ligament, Baudelot's ligament, extends from the lateral surface of the posterior end of the skull

laterally to and around the superior end of the cleithrum of the pectoral girdle to attach to the inner surface of the inferior end of the supracleithrum (pl. 1, fig. 2; pl. 2, fig. 2; pl. 3, fig. 2). The attachment of this ligament to the skull is in relation to the posterior margin of the auditory bulla. In the Myripristinae, Baudelot's ligament passes from the skull laterally over the junction between the antero-lateral projection and the body of the swim bladder. In *H. ascensionis* and *H. rufus*, its attachment to the skull is split just caudad to the posterior membranous area of the auditory bulla.

The retractor muscle of the upper pharyngeal jaw is also associated with this region. In all cases, the muscle takes origin from some sort of projection from the antero-ventral surface of the second centrum. In the Holocentrinae, generally this muscle is fleshy throughout. In *H. ascensionis* and *H. rufus*, because of the anterior bulges of the swim bladder, this muscle has an elongated, tendinous origin that lies in the groove between the two bulges. A short tendon, which is closely associated with the anterior surface of the swim bladder between the antero-lateral projections, serves as the beginning of this muscle in the Myripristinae. In each case, the condition of the pharyngeal jaw retractor muscle reflects the space available to it after the junction of the swim bladder to the auditory bulla has been accomplished.

E. *The Opisthotic Bone*

The opisthotic bone is one of the five basic ossifications in the otic capsule that forms the otic region of the skull in vertebrates. It is usually found in the posterior aspect of the otic region. In the Holocentridae, it is associated with the bony case of the horizontal (lateral) semicircular canal. It also has a bony process, which is connected through a ligamentous attachment to the inferior limb of the forked post-temporal bone.

In the Holocentrinae (pl. 1, fig. 3; pl. 2, fig. 3) the opisthotic bone is found to be a scale-like bone covering the posterior surface of the articulation between the exoccipital, prootic, and pterotic bones.

In the Myripristinae (pl. 3, fig. 4), on the other hand, the opisthotic bone is found to be an integral part of the otic wall. It has two parts: One, thin and elongate, extends along the posterior border of the exoccipital bone where it contains the horizontal semicircular canal. The other is an integral part of the postero-lateral corner of the cranium, articulating with the prootic, pterotic, and exoccipital

bones. This second, more substantial portion, bears the process for the inferior limb of the post-temporal bone.

DISCUSSION AND CONCLUSIONS

A study of the comparative morphology of the Holocentridae that includes the swim bladder, the auditory bulla, and the opisthotic bone indicates a clear-cut dichotomy of the genera within the family. In each of these three items the same genera fall clearly into the same one of two groupings.

The subfamily Myripristinae, one of the two groupings, includes the genera *Myripristis*, *Ostichthys*, *Holotrachys*, *Plectrypops*, and *Corniger*. In these, the swim bladder has antero-lateral projections that extend forward on either side of the posterior cranium. The medial walls of these projections are thinned and effect an intimate contact with the laterally facing membranous areas of the enlarged auditory bullae. The opisthotic bone is incorporated into the postero-lateral wall of the auditory capsule region of the cranium.

The subfamily Holocentrinae, the second of the two groupings, includes the genus *Holocentrus*. In this group, in general, the swim bladder is an elongated tube bluntly ended anteriorly, while the auditory bullae have their membranous areas facing laterally; no direct relationship with the swim bladder is effected. The opisthotic bone is a scale-like cover over the common articulation of the other bones forming the postero-lateral wall of the auditory capsule.

In the genus *Holocentrus*, however, two closely related species, *H. ascensionis* and *H. rufus*, have secondarily effected a direct relationship between the membranous areas of the auditory bullae and the swim bladder. The auditory bullae have become modified so as to be elongated posteriorly. At the same time the anterior end of the swim bladder is bulged forward on either side and is thinned out in the region of contact.

Starks (1908), while studying spiny-rayed fishes for communications between the swim bladder and the ear, examined *Holocentrus ascensionis* and *H. suborbitalis*. He noted this difference between the two species and erected a new genus, *Adioryx*, for *H. suborbitalis*, based upon this difference. The present study shows quite clearly that all of the species of the genus *Holocentrus*, excepting *H. rufus*, are of the general type and thus should be placed in the genus *Adioryx*, if Starks' classification were followed.

The relationship of the swim bladder to the ear suggests an auditory function. To date, however, to my knowledge, no work has been done on these fish to ascertain their "hearing" abilities. The anatomical relationships are those that are referred to in the literature as the direct connection, as differentiated from the indirect connection as seen in the Ostariophysi, wherein the swim bladder is connected to the ear by means of an ossicle chain. The intimate relationship to the sacculus is also in line with what is known in fishes that have increased "hearing" function through some sort of connection between the swim bladder and the ear.

SUMMARY

1. The swim bladder of the Myripristinae (*Myriptistis, Corniger, Ostichthys, Holotrachys,* and *Plectrypops*) is in direct relationship with the auditory bulla and the sacculus in particular through antero-lateral projections.

2. In the Holocentrinae (*Holocentrus*) in general there is no relationship between the swim bladder and the auditory bulla.

3. In two species of *Holocentrus* (*H. ascensionis* and *H. rufus*) a secondary connection is effected between the swim bladder and the auditory bulla.

4. These connections suggest an increased "hearing" ability in those species possessing the direct connection between the swim bladder and the auditory bulla.

LIST OF SPECIMENS USED

Specimen*	Museum number†	Number of specimens‡
HOLOCENTRIDAE:		82
Holocentrinae:		44
Holocentrus:		
(Holocentrus):		(10)
ascensionis	CNHM 44991, 46198, 48267, & unacc.	4
rufus (ascensionis)	CNHM 48118, 48234	4 (2)
rufus (meeki)	CNHM 48723, 49077	2
(Adioryx):		(24)
acus	USNM 52385	1
bullisi	CNHM 47921	1
caudimaculatus	USNM 52414	1
cornutus	USNM 146003	1
coruscus (tortugae)	CNHM 48639	1
diadema	CNHM 32811, 44131, 51367	4 (2)
lacteoguttatus	CNHM 44142	1
microstoma	CNHM 44124	1
punctatissimus	USNM 52199	1
suborbitalis	CNHM 19396, 26077, 41730, 50912	7 (4)
tiere	CNHM 44166	1
tiere (erythraeus)	USNM 93274	1
vexillarius	CNHM 26057	1
violaceus	USNM 139062	1
xantherythrus	CNHM 32819	1
(Sargocentron):		(5)
praslin	USNM 143336	1
praslin (ruber)	USNM 139060	1
spinifer	CNHM 44159	1
spinifer (unipunctatus)	CNHM 17948	1
tieroides	USNM 145870	1
(Flammeo):		(5)
laevis	CNHM 17920	1
opercularis	CNHM 44193	1
sammara	CNHM 44187, 44189	2
scythrops	USNM 126575	1
Myripristinae:		38
Myripristis:		(30)
species?	CNHM 50889, 50890	7 (7)
adustus	USNM 52404	1
argyromus	CNHM 44428, 44430, 49164	4 (1)
berndti	CNHM 44425	1
clarionensis	USNM 67573	1
jacobus	CNHM 19388	1
melanostictus	USNM 122928	1
microphthalmus	CNHM 17971, 17974, 17980, 44418	4

multiradiatus	CNHM 44350, 44352	2
murdjan	CNHM 44420, 44422	2
murdjan (intermedius)	CNHM 17956	1
occidentalis	CNHM 41518, 41790, 41792	3
pralinus	CNHM 44354	1
pralinus (sanguineus)	USNM 52207	1
Corniger:		(1)
spinosus	MCZ 4502	
Holotrachys:		(2)
lima	CNHM 4806, 441358	
Ostichthys:		(3)
japonicus	CNHM 55596, USNM 59804	2
trachypoma	CNHM 45431	1 (1)
Plectrypops:		(2)
retrospinus	CNHM 8382, 48643	

* Name in parentheses is name under which specimen is catalogued in museum.

† CNHM Chicago Natural History Museum
MCZ Museum of Comparative Zoology, Harvard University
USNM United States National Museum

‡ Number in parentheses is number used as microscopic sections.

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PLATES

Key to Abbreviations on Plates

SO, supraoccipitale
ExO, exoccipitale
BO, basioccipitale
PS, parasphenoidale
PrO, prooticum
SpO, sphenoticum
PtO, pteroticum
EpO, epioticum
OpO, opisthoticum

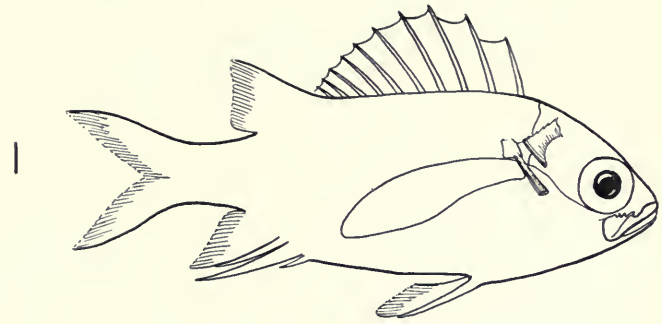
EXPLANATION OF PLATE

Holocentrus suborbitalis (CNHM 19396)

Fig. 1. An outline sketch to show the general relationships of the parts under consideration.

Fig. 2. A lateral view of the swim bladder–auditory bulla region. The auditory bulla is located in the postero-inferior corner of the cranium. Its membranous area faces laterad. The swim bladder ends anteriorly short of the skull. The retractor muscle of the upper pharyngeal jaw is fleshy throughout. Baudelot's ligament is a thickened portion of the anterior myoseptum and is associated with the posterior aspect of the auditory bulla.

Fig. 3. An oblique infero-lateral view of the posterior region of the cranium. The auditory bulla is made up primarily of the basioccipital, exoccipital, and prootic bones. The opisthotic bone is scale-like and overlies the articulation of the exoccipital, prootic, and pterotic bones.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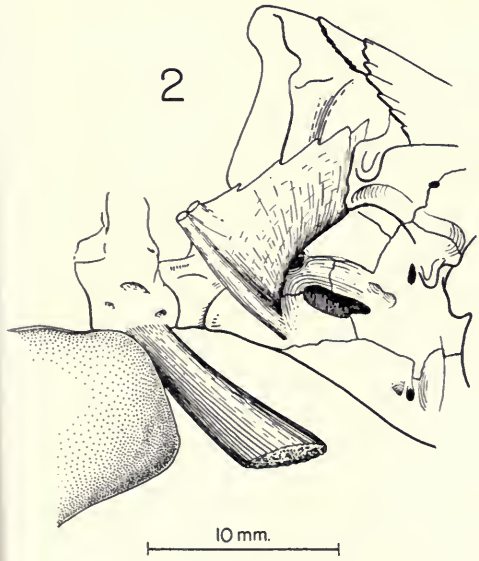
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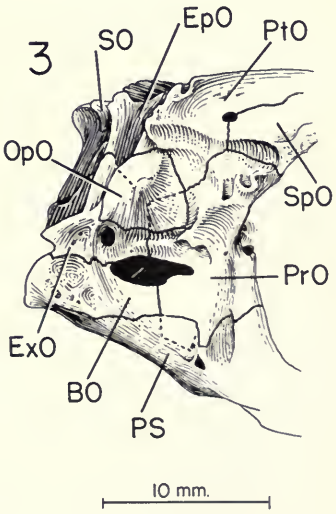
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EXPLANATION OF PLATE

Holocentrus ascensionis (CNHM 44991)

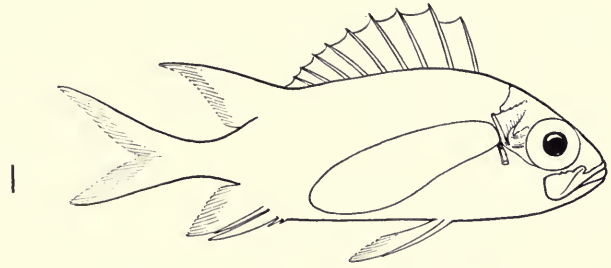
Fig. 1. An outline sketch to show the general relationships of the parts under consideration.

Fig. 2. A lateral view of the swim bladder–auditory bulla region. The swim bladder approaches the posterior end of the auditory bulla. The inferior thickening of the anterior myoseptum, Baudelot's ligament, is divided so as to allow the meeting of the thinned area of the swim bladder and the membranous area of the auditory bulla. The auditory bulla of this form has become elongated posteriorly in such a fashion as to have its membranous area facing posterad. The retractor muscle of the upper pharyngeal jaw has a tendinous origin as a result of this limitation of space.

Fig. 3. An oblique infero-lateral view of the posterior region of the cranium. Here, too, the auditory bulla is made up of the basioccipital, exoccipital, and prootic bones. The posterior elongation of the bulla has been accomplished primarily by modification of the prootic bone. The opisthotic bone is again scale-like, covering the articulation of the exoccipital, prootic, and pterotic bones.

Fig. 4. A view of the anterior end of the swim bladder. The centrum of the second vertebra and the retractor muscles of the upper pharyngeal jaws are *in situ* in relation to the swim bladder. The antero-superior portion of the swim bladder's *tunica externa* is thinned out where the swim bladder meets the membranous area of the auditory bulla.

Fig. 5. A view of the posterior end of the cranium. The membranous areas of the auditory bullae are seen inferiorly on either side of the infero-medial ridge formed by the basioccipital and parasphenoid bones. The scale-like character of the opisthotic bone is apparent.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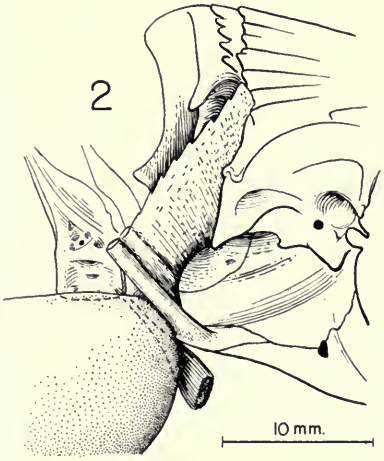
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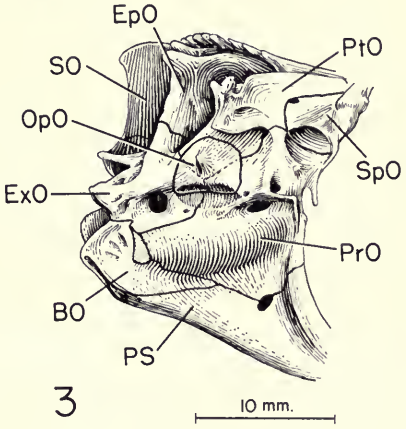
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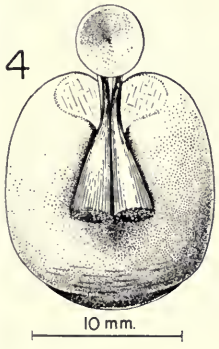
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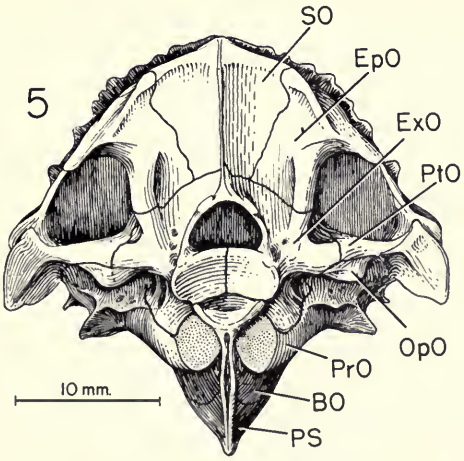
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EXPLANATION OF PLATE

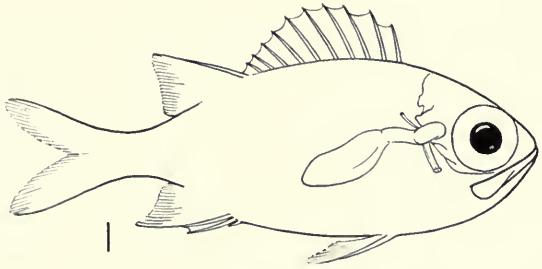
Myripristis argyromus (CNHM 44430)

Fig. 1. An outline sketch to show the general relationships of the parts under consideration.

Fig. 2. A lateral view of the swim bladder–auditory bulla region. The *tunica externa* of the anterior chamber of the swim bladder is attached to the centra of the anterior vertebrae. The antero-lateral projections extend forward on either side of the cranium so as to cover the auditory bullae. Baudelot's ligament extends laterad, crossing over the swim bladder at the junction of the antero-lateral projection with the anterior chamber, and continues on to the inferior end of the supracleithrum.

Fig. 3. A ventral view of the anterior end of the swim bladder. The constriction between the anterior and posterior "chambers" of the swim bladder is clearly seen. The antero-lateral projections bulge laterally and extend forward with their thinned-out areas facing mediad. The retractor muscles of the upper pharyngeal jaws are situated at the anterior end of the swim bladder between the antero-lateral projections and they originate from the centrum of the second vertebra by means of short tendons.

Fig. 4. An oblique infero-lateral view of the posterior region of the cranium. The auditory bulla is made up of the basioccipital, exoccipital, and prootic bones. The bony margins of the membranous area, however, are turned out laterally. In the case of this form the opisthotic bone forms an integral part of the otic region.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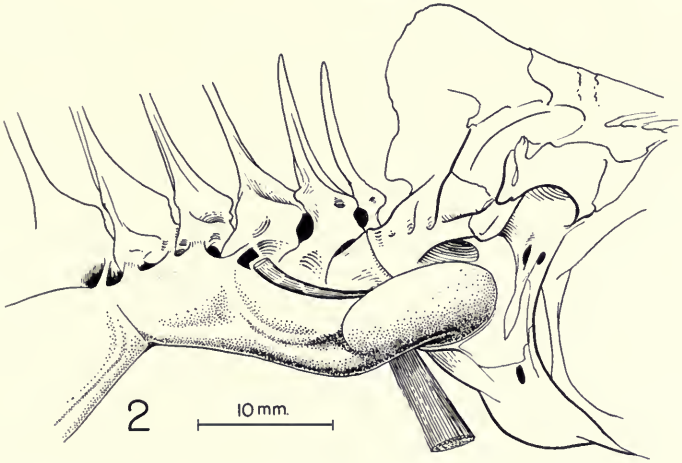
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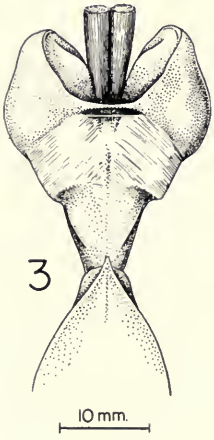
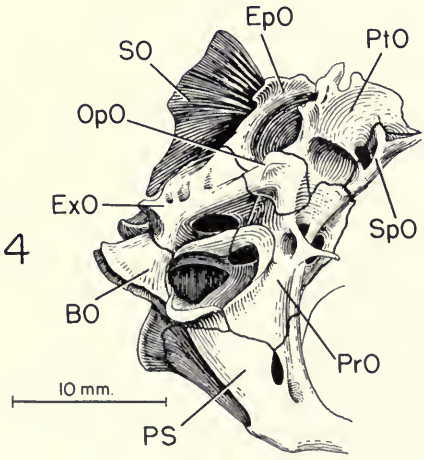

3
10 mm.


4
EpO
PtO
SO
OpO
ExO
SpO
BO
PrO
10 mm.
PS

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